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BIOLOGICAL BULLETIN.

NOTES ON MEROGONY AND REGENERATION IN RENILLA.

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H. B. Torrey¹ has published a brief note on regeneration in *Renilla* in which he shows that the young colonies possess a high regenerative capacity and records some valuable preliminary observations, but owing to the difficulty of procuring sufficient material he was unable to carry these observations far enough to reach a decisive result on some of the important questions concerned. During the summer of 1902, after repeated failures in preceding years, I was fortunate enough to secure at Beaufort, N. C.,² four lots of fertilized eggs from which hundreds of young colonies were reared (they were kept alive three weeks but produced only the two primary buds) and also a considerable number of older but still young colonies, obtained from the sand. I was thus able considerably to extend Torrey's experiments and also to make observations on the development of egg-fragments that yielded some suggestive results.

(a) THE DEVELOPMENT OF EGG FRAGMENTS.

All efforts failed to fertilize the eggs artificially, so that only fertilized eggs were available for experiment, but these can easily be cut individually with the scalpel into two or more pieces. As I showed in my paper of 1882³ the cleavage-nucleus divides several times (from three to five) before cleavage of the cytoplasm occurs, the egg usually segmenting, from two to three hours after it is laid,⁴ at once into eight or sixteen blastomeres

¹ "Some Facts Concerning Regeneration and Regulation in *Renilla*," *Biol. Bull.*, Vol. II., p. 6, 1901.

² I am indebted to the Hon. G. M. Bowers, U. S. Commissioner of Fisheries, for the privilege of occupying a table at the Beaufort laboratory, and to Dr. Caswell Grave, director of the laboratory, for his kind coöperation.

³ "The Development of *Renilla*," *Phil. Trans.*, Vol. III., p. 24.

⁴ As I found twenty years ago the eggs are always laid between 5:30 and 6 A. M.

(exceptionally into a larger number), though with many variations. Twenty-four eggs were cut, at intervals of three to ten minutes during the period between discharge and cleavage, into from two to five pieces that were isolated in water containing spermatozoa. Of these fragments at least one piece from each egg developed in all but one case. Of the first nineteen, covering a period of eighty-seven minutes only one piece from each egg developed (eighteen cases). These fragments divided like the whole eggs, and at the same time with the latter (two and one half hours), into approximately eight or sixteen blastomeres. Of the five remaining cases two or three pieces from each egg developed, segmenting in such a way that the total number of blastomeres formed from each egg was at least approximately, and probably accurately, the same as those produced from an entire egg. The number of the blastomeres in the segmenting fragments of the respective eggs (which, owing to lack of time, could not be exactly counted) were approximately $4 + 12$, $4 + 12$, $4 + 8$, $4 + 5 + 16$, $4 + 12$. These results are what would have been expected. It is evident that the development of only a single piece in the earlier period is due to the fact that the egg still contains only a single nucleus; and only when the nucleus has divided one or more times does the possibility arise of obtaining more than one nucleated piece from a single egg. The facts seem worth recording, as showing that, despite the absence of a fertilization-membrane after fertilization has occurred, non-nucleated pieces of the egg cannot be again fertilized (which agrees with my later experiments on *Cerebratulus*, an account of which is now in press); and also that the period at which cleavage occurs does not depend on the number of nuclei in the piece but on some other progressive change which reaches the critical point at the same time whether the egg be cut to pieces or remain a whole.

Of more general interest is the fact that egg fragments not more than one fourth the bulk of the egg may develop into dwarf larvæ, which, after swimming for the normal period (about forty-eight hours), sink to the bottom, develop tentacles, and *produce the first pair of buds in normal fashion*. Thus arise dwarf colonies of various sizes that are, in every detail, miniatures of the normal colonies of the same age. Fig. 1 shows side

by side three colonies eight or nine days old, the largest being the product of a whole egg, the smallest that of a fragment about one fourth the size of a whole egg, and the third that of half an egg. These drawings are from camera sketches that show very nearly the true proportions, though owing to the occasional movements of the animals the details had to be drawn free hand. Allowing for slight differences in the state of expansion it may

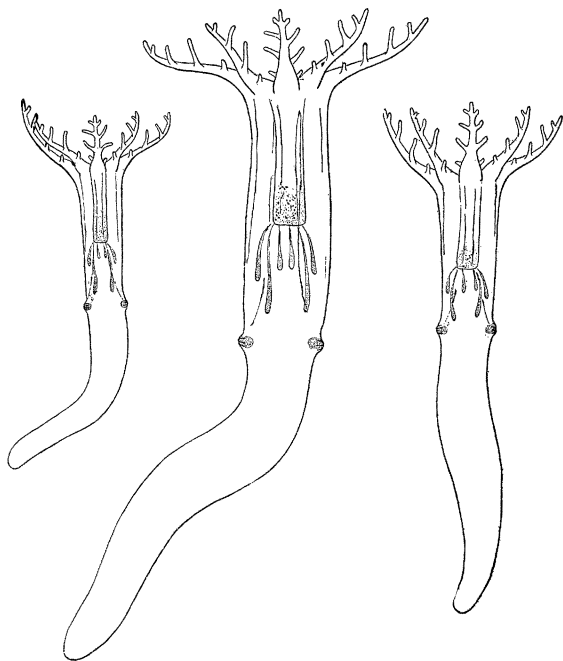


FIG. 1. In the middle, primary polyp with first pair of buds, reared from an entire egg, eight days. To the right and left are dwarf colonies nine days old drawn to the same scale, from fragments of fertilized eggs, one of approximately one half, the other of one fourth the bulk of an entire egg.

be seen that the dwarfs are very exactly similar to whole colonies of reduced proportions. Beyond this stage it was not found possible to rear the young colonies, even after three weeks, probably owing to the difficulty of providing the animals with suitable food.

These results are of some interest as proving that in this case the process of budding does not depend on the attainment of a certain size-limit by the parent stock, but on that of a definite ontogenetic stage, exactly as if the buds were organs of a single individual. It can hardly be doubted that in the ancestral type

the buds were set free from the stock, as still occurs in many polyps. Here, however, their individuality has become completely merged in that of the organism as a whole, which develops, as it behaves in the adult condition, essentially as a unit, the bud-formation in the merogonic development being subject to a process of regulation in a manner precisely analogous to the formation of organs in the development of a dwarf pluteus or pilidium from an egg fragment. This conclusion, which is also reached from the facts of regeneration described beyond, is not without a broader interest in its bearing on the possible derivation of metameric animals from linear colonies, or even on the relation of Metazoa to colonial Protozoa.

(b) DEVELOPMENT OF FRAGMENTS OF PLANULAS.

I made a few experiments by cutting to pieces the spherical planulas of two to four hours (consisting of 128 cells or more) which are placed on record as suggesting the interest of more extended studies of the same kind. Like fragments of the unsegmented eggs, the planula fragments quickly round out and continue their development for a time apparently unimpaired, and in this way were obtained from a single egg several swimming planulas—in one case nine from a single egg, in one case six, in two cases five, and two or three from the remainder. Though only seven planulas were thus operated the results seem to show that at this period the power of regulation is already somewhat diminished. Of the thirty-one fragments obtained only two developed into normal dwarf colonies. All the others produced abnormal or defective larvæ, the most abnormal ones, as was to be expected, arising from the smaller fragments. Some failed to form stomodæum or septa, others produced stomodæum and the normal number of mesenteries, but no peduncle, several were nearly normally formed but produced no buds, and only a single pair of mesenterial filaments, one produced only a single large median bud, while several of the smaller larvæ showed less than the normal number of mesenteries. Of the nine fragments of a single planula six ultimately died, but the remaining three pieces, including the two largest, developed into larvæ all of which possessed stomodæum and mesenteries. The smallest

of these formed no tentacles, peduncle or mesenterial filaments, and only four mesenteries. Both the other two developed six mesenteries and rudimentary tentacles, one pair of short mesenterial filaments; only one of them formed a peduncle. This case indicates that the number of mesenteries is not specified at this period; for although none of the larvæ produced the full number the total number formed from the original egg was sixteen.

(c) EXPERIMENTS ON REGENERATION IN THE YOUNG COLONIES.

My principal object in studying the young colonies was to examine the relation between morphallaxis and neomorphosis (to adopt Morgan's terms) for which purpose such an organism as *Renilla* offers obvious advantages, and also to ascertain, if possible, how far the process of bud-formation is capable of regulation. The main results reached by Torrey were: (1) That the polarity of the primary polyps was never reserved, a polyp always regenerating at the anterior end of a piece and a peduncle at the posterior end; (2) that the power of regeneration was confined to the budding zone; (3) that after oblique section, a remoulding of the old parts occurred by a regulation "in a plastic fashion," but he did not succeed in following the later changes long enough to ascertain whether this plastic remoulding was permanent, and involved the establishment of a new axis of symmetry. Like Torrey, I found that when the peduncle was removed, at any level, a new peduncle very quickly reappeared; that removal of the axial polyp by transverse section led to regeneration of that polyp; and that as a rule a severed peduncle did not regenerate a new axial polyp at the anterior end; and that by oblique section through the budding zone two colonies might be produced from one. On some points, however, my results differ from his, while they give a pretty definite answer to the undecided question regarding the phenomena of remoulding.

1. In a single case a reversal of polarity was obtained from a colony having five buds that was cut into three pieces by sections anterior and posterior to the budding zone as shown in Fig. 2, A. As a rule after operations of this type, only the middle piece, containing the budding zone, regenerates a perfect colony,

a new peduncle being formed posteriorly and a new axial polyp anteriorly, while neither the severed axial polyp nor the peduncle regenerates, though both may live for a sufficient period of time (in some cases a week or more). In this instance the peduncle, as usual, failed to regenerate, while the middle piece regenerated an axial polyp in front and peduncle behind. The anterior piece (2 *B*) formed an exception to the rule in that it regenerated a large polyp at the posterior end, a form being produced with two similar polyps united at the base and point-

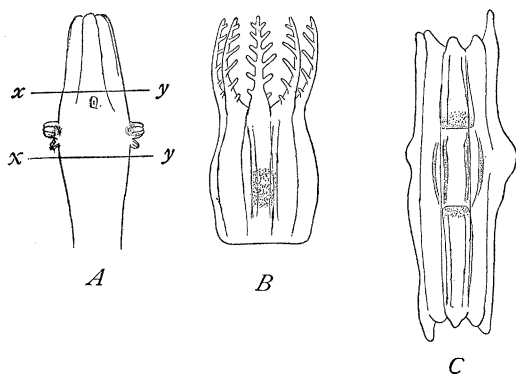


FIG. 2. *A*, outline of young colony with two pairs of buds, in the contracted state, showing planes of section. *B*, the anterior piece (axial polyp), twenty-four hours later; the middle piece already showed a new axial polyp and peduncle well under way. *C*, the anterior piece fifteen days after the operation, with new polyp at base, and the original tentacles reduced.

ing in opposite directions (Fig. 2, *C*). Each possessed a stomodæum, and the mesenteries were continuous from one to the other, bearing six mesenterial filaments. At one side was a rounded elevation that may have been a regenerating peduncle; but the animal died without further change. An interesting feature of this case was the degeneration of the original tentacles, which lost their pinnules and became greatly shortened so as to form rudiments closely similar to those of the regenerated polyp, or those of an early larva. I have observed the same phenomenon in young colonies in which the peduncle, after its removal and regeneration, had been again successively twice removed and regenerated, the whole animal having been in the meantime considerably reduced in size. This shows that regeneration takes place at the cost of material throughout the colony, even involving regressive

changes in parts already completely formed. Interesting results can doubtless be obtained by the further study of these changes.

2. The above case not only shows a reversal of polarity but proves that regeneration may take place anterior to the budding zone. A similar result was also given in several cases where the peduncle was removed by section posterior to the budding zone ; but this only occurs when the section is not far removed from the budding zone.

In at least one such case it is certain that the section was outside the normal limits of the budding zone, the colony having

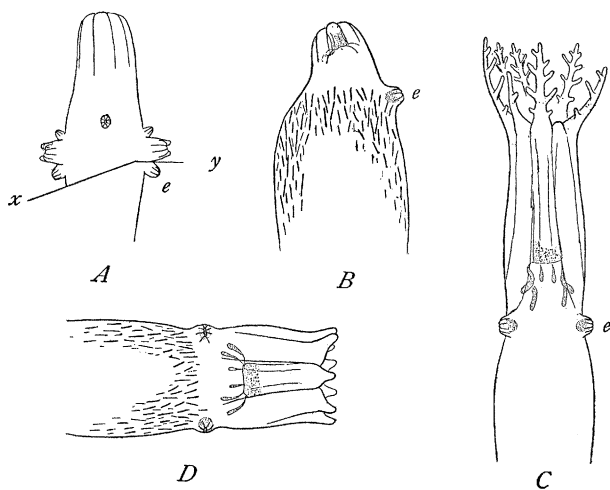


FIG. 3. *A*, outline of young colony with three pairs of buds, showing plane of section. *B*, posterior piece after forty-eight hours, with new axial polyp forming ; a new peduncle had formed on the anterior piece. *C*, the same nine days later, with nearly perfect axial polyp and new bud on the left side. *D*, new axial polyp and pair of buds regenerated from the anterior end of a peduncle, cut off behind the budding zone from a young colony with seven pairs of buds ; five days after operation.

seven buds on each side. In two days a new axial polyp was well under way at the anterior end of the severed peduncle. In five days this polyp was well developed, with short tentacles and mesenterial filaments, while a pair of symmetrically placed buds had appeared in the same position as in the young colonies (Fig. 3, *D*). A condition was thus attained essentially similar to that of the young colonies developed from the egg (*cf.* Fig. 1), though the peduncle was of course greatly exaggerated in

relative size. This colony died eight days after the operation without further change except further development of the axial polyp.

3. Experiments to test the degree of specification of the persons of the polymorphic colony, and the relation between morphallaxis and neomorphosis, while not absolutely conclusive, give strong ground for the conclusion that, despite a limited power of heteromorphosis and regulation, as shown by the foregoing experiments and those of Torrey, the individual persons are on the whole definitely specified in respect both to the rate of growth and to their axial relations to the colony as a whole. To test this I first tried to see whether the removal of the large buds would result in the more rapid development of the remaining small buds. For this purpose colonies were cut in such a way as to leave only a single small bud attached to the peduncle (Fig. 3 *A*). Since this bud (*e*) is destined to develop into a polyp like the axial one it might have been expected that it would develop at once into a new axial polyp. The fact is quite to the contrary, for the small bud remains stationary while a new axial polyp is produced at the front end of the peduncle (Fig. 3, *B*, *C*). In one case, indeed, the small bud completely disappeared during the process, being apparently absorbed, the whole growth-energy having concentrated in the regenerative process. In the individual figured the small bud remained wholly unchanged while a new axial polyp was regenerated (slightly abnormal in respect to the tentacles), but in the meantime a second bud was formed in the corresponding position on the opposite side of the body; so that the young colony attained the same condition (Fig. 3, *C*) as in Fig. 3, *D*. The comparison of these two cases is interesting, since the same condition was obtained by different methods, both buds being formed anew in the one, while in the other only one bud was produced to form the fellow of the existing one. This indicates that the characteristic first stage in the normal development, with a single pair of buds (Fig. 1) is a definite ontogenetic stage that represents, as it were, a condition of equilibrium that is first restored after the operation before a second step is taken. A definite morphological relation therefore exists between the persons of the

colony that seems exactly comparable to that existing between the different organs of a single individual — essentially the same result as that given by the formation of dwarf colonies from egg fragments.

I endeavored to see whether, by removing all the buds except the exhalent zoöid, this rudimentary person could be made to

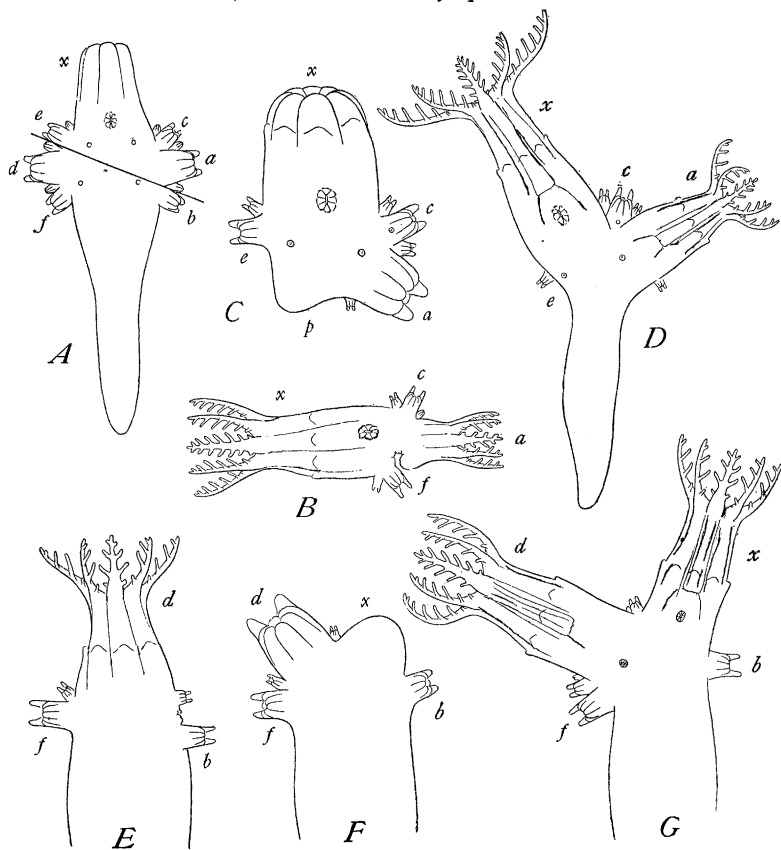


FIG. 4. Regeneration after oblique section. *A*, outline of colony (contracted) with six pairs of buds, showing plane of section. *B*, anterior piece, four hours after operation; after twelve hours the wound had entirely closed. *C*, the same forty-eight hours after operation, showing rudiment of peduncle. *D*, the same five days after operation; return of lateral bud to its original position. *E*, posterior piece, twenty-four hours after operation; lateral bud in the former position of the axial polyp. *F*, the same twenty-four hours later; new axial polyp (*X*) forming. *G*, the same, seven days after operation; new axial polyp well developed, with new exhalent zoöid; return of lateral bud nearly to its original position. During the following ten days the axial polyp became as large as the lateral one, but no other buds were formed.

develop into a fully developed polyp. None of these cases lived more than six days, but in one of them the exhalent zoöid had very considerably enlarged. This may, however, have been a merely passive expansion, and I regret that no decisive result was reached. Repetition of Torrey's experiment of cutting the colony diagonally across at an angle of 45° gave a suggestive but not quite conclusive result. The best case obtained is shown in Fig. 4, the section being in such a plane as to leave one of the primary lateral buds (a, d') in each piece, the posterior piece having in addition four smaller buds and the anterior one six. Within an hour after the operation, and while the wounds were still widely open, a complete readjustment had occurred in the relative position of buds, and after twelve hours the wounds were entirely healed. The large lateral bud (d) of the posterior piece was so displaced as to be directed straight forward, giving exactly the appearance of an axial polyp (Fig. 4, E), while by a corresponding process in the anterior piece the lateral bud (a) was directed straight backward (4, B). In the course of 48 hours however a rapid formation of new tissue took place in both pieces, forming the beginning of a new axial polyp in the posterior piece (4, F) and of a new peduncle in the anterior one (4, C). At the end of seven days the new axial polyp of the posterior piece (4, G, x) was fully formed though still not quite as large as the original lateral one, with four pairs of tentacular pinnules, and a median dorsal bud had appeared exactly in the position of the exhalent zoöid. When the colony was fully expanded the new axial polyp was directed almost straight forward while the original lateral bud (d) was swung quite over to one side, nearly in its original position, though the colony still showed a very marked asymmetry. At the end of seventeen days the axial polyp was as large as the lateral one, but no other essential change had occurred. The colony was at this time killed for preservation, since I was compelled to leave Beaufort; but the evidence of the specification of the buds obtained from this and the other cases described renders it probable that the original condition would ultimately have been restored and that the primary process of moulding would in the end have been wholly overcome by the regenerative process. In the meantime

the anterior piece (4, *D*) had generated a long peduncle, from the anterior end of which the original axial polyp and right lateral one diverged as shown in the figure.

This case shows with great clearness that very soon after the operation the fragment is plastically remoulded, in a manner somewhat similar to that described by Hargitt and Morgan,¹ in the medusa *Gonionemus*, so that without the formation of new tissue the pieces assume a new condition of equilibrium which in the posterior piece brings a lateral polyp into the former position of the axial one. This process takes place so quickly that it seems inadmissible to suppose that it is due to an active process of growth. It gives rather the impression of a mechanical process due to the operation of purely physical factors (tension of the tissue or the like) by which a new condition of equilibrium is restored as nearly as possible like that of an entire colony, and hence representing a case of pure "mechanical regulation" in the sense in which Child has construed the primary process of morphallaxis in planarians.² Broadly speaking this process is probably of the same nature as that by which the edges of a cut surface close, though in both pieces the change of form was already complete while the wound was still widely open, as may be seen from Fig. 4, *B*. As such, it cannot be considered as part of the regenerative process in the strict sense,³ indeed this is proved by the fact that the ensuing regeneration gradually counteracts the effect of the initial remoulding. I can, however, find no ground in Morgan's own discussions for excluding such a mechanical remoulding of the old parts from the conception of morphallaxis in general, and the same ground is taken in the case of *Stenostoma* by Child, who reaches the conclusion that morphallaxis in this form is "essentially a change in form resulting from differences in mechanical tension in the piece as compared with the whole" ('02, p. 414). The facts of initial morphallaxis observed in *Renilla* fall in very well with Morgan's tension-hypothesis, and

¹ C. W. Hargitt, "Recent Experiments on Regeneration," *Zoöl. Bull.*, I., 1897.
T. H. Morgan, "Regeneration in the Hydromedusa *Gonionemus*," *Am. Nat.*, XXXIII., 1899.

² C. M. Child, "Fission and Regulation in *Stenostoma*," *Arch. Entom.*, XV., 2, 3, 1902.

³ Cf. Morgan, "Regeneration," p. 69.

the remarkable quickness of the process is doubtless due to the extremely plastic character of the tissues in the animal, ordinarily shown in its frequent and very marked changes of form. In planarians the initial remoulding takes place much more slowly and forms an initiative for other regulative changes by which the piece is permanently remodelled into a new form. In *Renilla* such regulative changes are apparently absent, or present in only small degree, and the ensuing process of neomorphosis tends to counteract the initial morphallaxis and restore the original form. Morgan¹ has shown that even two species of the same genus may differ materially in the ratio between remoulding of the old tissues and the formation of new, the latter process being more extensive in *P. lugubris* than in *P. maculata*. *Renilla* appears to offer a case in which both processes occur, but the former produces a result that is only temporary, owing to a high degree of specification in the members of the colony. That this specification is, however, not absolutely fixed is evident from the fact that heteromorphosis may occur, as shown in the formation of a new peduncle from a lateral group of polyps (Torrey), or in the development of a polyp instead of a peduncle from a severed axial polyp; and the same is proved by the establishment of a new colony after removal of the budding zone, as recorded above.

ZOOLOGICAL LABORATORY OF COLUMBIA UNIVERSITY,
January 15, 1903.

¹T. H. Morgan, "Growth and Regeneration in *Planaria lugubris*," *Arch. Entw.*, XIII., 1, 2, 1901.